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A New Nonmammalian Eucynodont (Synapsida: Therapsida) from the Triassic of Northern Gansu Province, China, and its Biostratigraphic and Biogeographic Implications

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ABSTRACT

A new trirachodontid eucynodont, *Beishanodon youngi*, is named and described based on a well-preserved skull from Triassic lacustrine deposits exposed in the Beishan Hills, northern Gansu Province, China. The new discovery documents the second record of trirachodontid eucynodonts known from China, along with *Sinognathus gracilis* from the Middle Triassic Ermaying Formation exposed in Shanxi Province. Cladistic analysis supports the placement of the new taxon as the sister group of *Sinognathus*, and the two together can be classified in Sinognathinae, a new subfamily differentiated from other trirachodontids by possession of several derived character states, including extremely short snout and strongly expanded temporal region. In addition, the stratigraphic and biogeographic significance of the new discovery are discussed. Because trirachodontids have a restricted stratigraphic range in the Triassic, as best documented by the *Cynognathus* Assemblage Zone of South Africa, discovery of the new fossil of this group from northern Gansu Province in China provides definitive evidence for a Triassic age of the fossil-bearing beds exposed in the Beishan Hills; moreover, the fossil beds are assessed as Early Triassic in age based on the evidence from the entire vertebrate fauna.

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INTRODUCTION

Nonmammalian cynodonts are a group of advanced therapsids that flourished during the Triassic and are of particular phylogenetic significance because of their close relationship to mammals. Cynodonts that are more derived than *Thrinaxodon* and other basal forms are classified together as Eucynodontia (Kemp, 1982; Hopson, 1991; Rubidge and Sidor, 2001; see also Abdala et al., 2006), characterized by shared derived features as follows: the dentaries are enlarged and fused at the symphysis; the postdentary bones are reduced in size; a supplementary surangular-squamosal contact is established lateral to the quadrate-articular jaw articulation; an acromion process is developed on the leading edge of the scapula; and the mammalian phalangeal formula (2.3.3.3.3) is achieved in both manus and pes (Rubidge and Sidor, 2001). Widely distributed across the ancient supercontinent Pangaea, several families of eucynodonts are important faunal components in continental beds of Triassic age in Africa, Madagascar, South America (Argentina and Brazil), Antarctica, and Eurasia. Because of their short geologic range and wide geographic distribution, eucynodonts have contributed significantly to Triassic nonmarine intercontinental correlation and paleobiogeographic reconstruction (Rubidge and Sidor, 2001). Of Triassic eucynodonts, the biostratigraphic utility of the gomphodont family Trirachodontidae is of special interest in that its included taxa document rapid morphological evolution within a brief temporal interval across an extensive geographical range, from southern Africa (South Africa, Namibia, and Tanzania) to eastern Asia (China) (Rubidge and Sidor, 2001; Abdala et al., 2006): regardless of where they occur, all known trirachodontids are limited to beds of Olenekian-Anisian age (Early to Middle Triassic, 250–237 Ma; Abdala et al., 2006). In addition to their interest to biostratigraphers, trirachodontids have also been the focus of recent studies centering on aspects of their paleobiology, including the patterns of growth that they exhibit (e.g., Botha and Chinsamy, 2004) and their possible communal life in warrens (Groenewald et al., 2001; Smith and Swart, 2002).

The present paper reports the discovery of a new Early Triassic trirachodontid eucynodont

from richly fossiliferous beds exposed at a locality in the Beishan Hills, northern Gansu Province, China (Gao et al., 2004, 2005; fig. 1). The fossil-bearing beds at this locality are dark shales of apparent lacustrine origin deposited in an intermontane graben environment. In addition to the trirachodontid, this locality has also yielded the remains of diverse other vertebrates, including several kinds of fishes (hybodont sharks, actinopterygians, and coelacanths), lepospondyl and aquatic temnospondyl amphibians, and a lizardlike reptile (Gao et al., 2004, 2005). Some of the fish fossils belong to taxa that are geologically time sensitive. These include *Boreosomus*, a lower actinopterygian that is known only from the Early Triassic, though it is widely distributed, with occurrences in Spitsbergen, Greenland, western Canada, and Madagascar (Schaeffer and Mangus, 1976), and now an unequivocal record from China (Xu and Gao, 2007). A second actinopterygian at the Beishan locality is identified as *Perleidus* (Xu and Gao, 2007), which had a cosmopolitan distribution during the Triassic (Battail et al., 1987; Beltan, 1988; but see also Lombardo, 2001). In addition to the vertebrate assemblage, the Beishan locality has yielded fossil plants, including *Neocalamites* (Triassic horsetails), lycopsids, and ginkgophytes (D. Wang, research in progress). Collectively, the vertebrates and plants from this locality indicate deposition under freshwater conditions during Early Triassic time (Gao et al., 2004, 2005). Because of the limited stratigraphic range of trirachodontids worldwide, the new trirachodontid, known from a well-preserved skull, provides a definitive age for the Beishan site and its contained fossils.

Before the fossil discovery from Gansu, the only previously known trirachodontid from China was *Sinognathus gracilis* from the upper part of the Ermaying Formation (Anisian; China National Committee for Stratigraphy, 2001) exposed in the Wuxiang area (fig. 1), Shanxi Province (Young, 1959; Sun, 1988). This species, documented by a skull with lower jaws (IVPP V2339), was originally included in the family Cynosuchidae and was interpreted as possibly a close relative of the South African cynodont *Thrinaxodon* (Young, 1959). Hopson and Kitching (1972) questioned Young's taxonomic assignment and treated the genus as

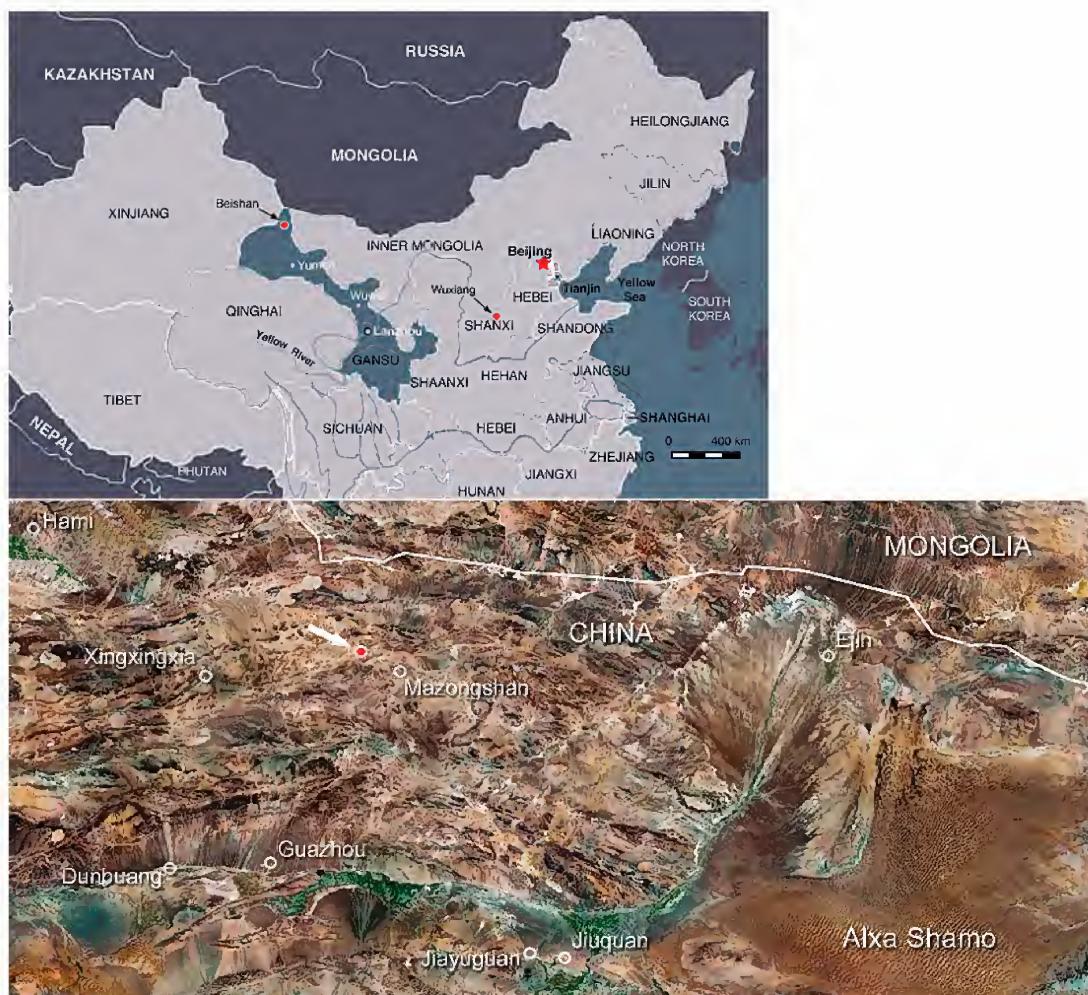


Fig. 1. Map of China (above) showing the geographic location of the fossil locality in the Beishan Hills, northern Gansu Province, in relation to the Wuxiang locality in the Shaanganning Basin. Satellite photo of the Beishan area (below); the white arrow points to the type locality (41°56'739"N/96°32'023"E) in the Beishan Hills (satellite image from Google.com).

“Trirachodontinae incertae sedis.” Later study, based on further preparation of the specimen, revealed dental characters that confirm its trirachodontid relationship (Sun, 1988). Abdala et al.’s (2006) recent review of trirachodontids recognized the trirachodontid affinities of *Sinognathus* but excluded it from their phylogenetic analysis, which was limited to Gondwanan gomphodonts.

A possible trirachodontid from Eurasia is *Neotrirachodon expectatus* from the Middle Triassic Donguz Formation, Orenburg region, in southeastern European Russia (Tatarinov,

2002). The holotype (PIN 2865/595) of this taxon is an incomplete left lower jaw with teeth. The specimen was first assigned to *Antecosuchus ochevi* (Tatarinov, 1973, 1988), but later was designated as the holotype of *Neotrirachodon expectatus* in the family Trirachodontidae (Tatarinov, 2002). However, other studies have either treated the problematic taxon as “Gomphodontia incertae sedis” (Abdala et al., 2006) or more likely to be a bauriid thecocephalian (Battail and Surkov, 2000; James Hopson and Bruce Rubidge, personal commun., 2008).

ABBREVIATIONS

Institutional

IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing
PIN	Paleontological Institute, Academia Nauk, Moscow
PKUP	Peking University Paleontological Collections, Beijing

Anatomical

cec	central cusp
ect	ectopterygoid
ept	epipterygoid
fr	frontal
inf	incisive foramen
ju	jugal
lac	labial cusp
lcr	lacrimal
lcrf	lacrimal foramen
lic	lingual cusp
m	maxilla
mpf	major palatal foramen
mxf	maxillary foramen
na	nasal
pa	parietal
pal	palatine
par	parasphenoid
pcf	paracanine fossa
pm	premaxilla
po	postorbital
ppr	paroccipital process
prf	prefrontal
ptg	pterygoid
qj	quadratojugal
qu	quadrate
sm	septomaxilla
sq	squamosal
vo	vomer

GEOLOGICAL SETTING

The Triassic fossil beds exposed in the Beishan Hills, which include the type locality of the new taxon *Beishanodon youngi*, represent a previously unrecognized lithostratigraphic facies in the nonmarine Triassic System of China. In terms of regional geology, these beds occur within the Beishan Minor Region of the Northern Xinjiang–Beishan Mountains Stratigraphic Region (Yang et al., 1982, 2000; Yin, 2003: Central Asia Region). At present nonmarine Triassic deposits within the Beishan Minor Region are referred to the

Erduanjing and Shanhujing formations (Bureau of Geology and Mineral Resources of Gansu Province, 1989). The Lower and Middle Triassic Erduanjing Formation consists of purplish-red coarse clastics (conglomerates and sandstones), while the Upper Triassic Shanhujing Formation is composed of gray to grayish-green coarse sandstones and siltstones containing plant fossils *Danaeopsis fecunda* and *Bernoullia zeilleri*? (Bureau of Geology and Mineral Resources of Gansu Province, 1989, 1997). Both formations are lithologically distinct from the Beishan fossil beds, and thus, the names of these units are inapplicable to them.

Deposits resembling the dark shales of the Beishan beds are exposed at Hongyanjing (section position at 96°11'E, 44°48'N; approximately 30 km northwest of the Beishan site) and have been dubbed the Hongyanjing Formation (Bureau of Geology and Mineral Resources of Gansu Province, 1989, 1997). The age of the Hongyanjing Formation has been interpreted as Late Permian based on the plants *Callipteris zeilleri*, *Callipteris ivanoevia*, and *Glottophyllum cuneatum* (Bureau of Geology and Mineral Resources of Gansu Province, 1997). However, increasing recent evidence has shown that traditional usage of the form genus *Callipteris* as an index fossil for the Permian is highly problematic. This situation is worsened with the discovery of the generic name *Callipteris* Brongniart, 1849, as a later homonym of *Callipteris* Bory 1804 (a genus of extant ferns; see Kerp and Haubold, 1988, for taxonomic history and comments). As a consequence of a major taxonomic revision, *Callipteris zeilleri* and *Callipteris ivanoevia* have been placed in a long list of species dubiae in Kerp and Haubold (1988). Nonetheless, similar plant fossils, including “*Callipteris*” *zeilleri*, are now known from the Beishan beds (J. Wang and D. Wang, personal commun., 2008), implying that the Beishan beds are stratigraphically correlative to the dark shales exposed in the Hongyanjing area. Based on lithologic similarity, we suggest that the name Hongyanjing Formation is appropriate for the Beishan fossil beds, but from the vertebrate index fossils that they contain (see discussion below), we consider the age of at

least the dark shale deposits at the Beishan site to be Lower Triassic.

Triassic deposits known from northern China are predominantly red clastics developed in a series of intermontane grabens and fluviolacustrine basins, including the Junggar, Turpan-Hami, and Yining basins. The Lower Triassic red beds in these basins comprise the Jiucaiyan and Shaofanggou formations (Cangfanggou Group) and contain the *Lystrosaurus-Sinokannemeyeria* vertebrate fauna (Yang et al., 2000). The Middle Triassic beds are known as the Karamay Formation (Yang et al., 2000; Yin, 2003), containing the *Parakannemeyeria* fauna (Yang et al., 2000). The fossiliferous dark shales exposed in the Beishan Hills, east of the Turpan-Hami basins, are sharply in contrast to the characteristic red beds of this stratigraphic region in both lithological features and faunal components. The dark shales are of variable thickness (maximum thickness of 300 mm at Quarry-3) and are part of a succession of sedimentary rocks that rests nonconformably on Hercynian plagioclorites (fig. 2). The lithologic and biostratigraphic features of the Beishan fossil beds strongly indicate a depositional environment that is sharply different from the Triassic red beds known in the nearby stratigraphic regions, including the Northern Xinjiang–Beishan Mountains Stratigraphic Region (Yang et al., 1982) and the Shaanxi-Gansu-Ningxia Basin (Shaanganning Basin), in which the Early Triassic beds are composed of the Liujiagou and Heshanggou formations. Evidently, the Triassic beds in the Beishan Hills were formed in depositional facies previously unknown in the terrestrial Triassic System of China.

Besides representing sharply different depositional facies from that of the contemporaneous redbeds in the nearby Xinjiang area and Shaanganning Basin, the dark shales exposed in the Beishan Hills have no traceable lateral continuity with them; therefore, the formational names such as “Jiucaiyan” and “Shaofanggou” in Xinjiang or “Liujiagou” and “Heshanggou” in the Shaanganning Basin are inapplicable for the fossil beds cropping out in the Beishan Hills.

The lithological features and associated fauna from the Beishan Quarry clearly point to a

lacustrine depositional environment. The fossil-bearing dark shales as cited above are composed of weathered silty detritus derived from metamorphic rocks (J.F. Lerbekmo, personal commun., 2004), whereas the associated fauna consists mostly of aquatic vertebrates accompanied by a few individuals representing terrestrial forms. Specimens of a hybodont shark have well-preserved soft-tissue impressions of whiskerlike narial and oral barbels, and comparisons of these structures with their analogues in extant sharks suggest that the hybodont was a sluggish bottom feeder (Steel, 1985). Exceptionally detailed preservation of soft-tissue structures in all the hybodont specimens from the Beishan Quarry reflects in situ deposition and fossilization of the specimens. This same excellence of preservation is seen in the actinopterygians (represented by several thousand specimens) and amphibians (a small temnospondyl and two microsaur lepospondyls) also from the Beishan Quarry. The undescribed temnospondyl, known from over 300 specimens, is neotenic, with many individuals showing both heavy ossification of the skeleton, an adult feature in amphibians, and gill rakers, found otherwise only in unmetamorphosed aquatic larvae. Larval amphibians are unambiguous indicators of freshwater environments. In contrast, the trirachodontid eucynodont described in this paper (known from a single specimen), the lepospondyls (known from five specimens), and the lizardlike diapsid (known from only three specimens), are probably allochthonous faunal components that were serendipitously washed into the Beishan Lake from nearby terrestrial habitats.

SYSTEMATIC PALEONTOLOGY

SUBCLASS SYNAPSIDA OSBORN, 1903

ORDER THERAPSIDA BROOM, 1905

SUBORDER CYNODONTIA OWEN, 1861

INFRAORDER EUCYNODONTIA KEMP, 1982

FAMILY TRIRACHODONTIDAE CROMPTON, 1955

SINOGNATHINAE, NEW SUBFAMILY

SUBFAMILIAL CONTENTS: The type genus plus the new genus and species described herein.

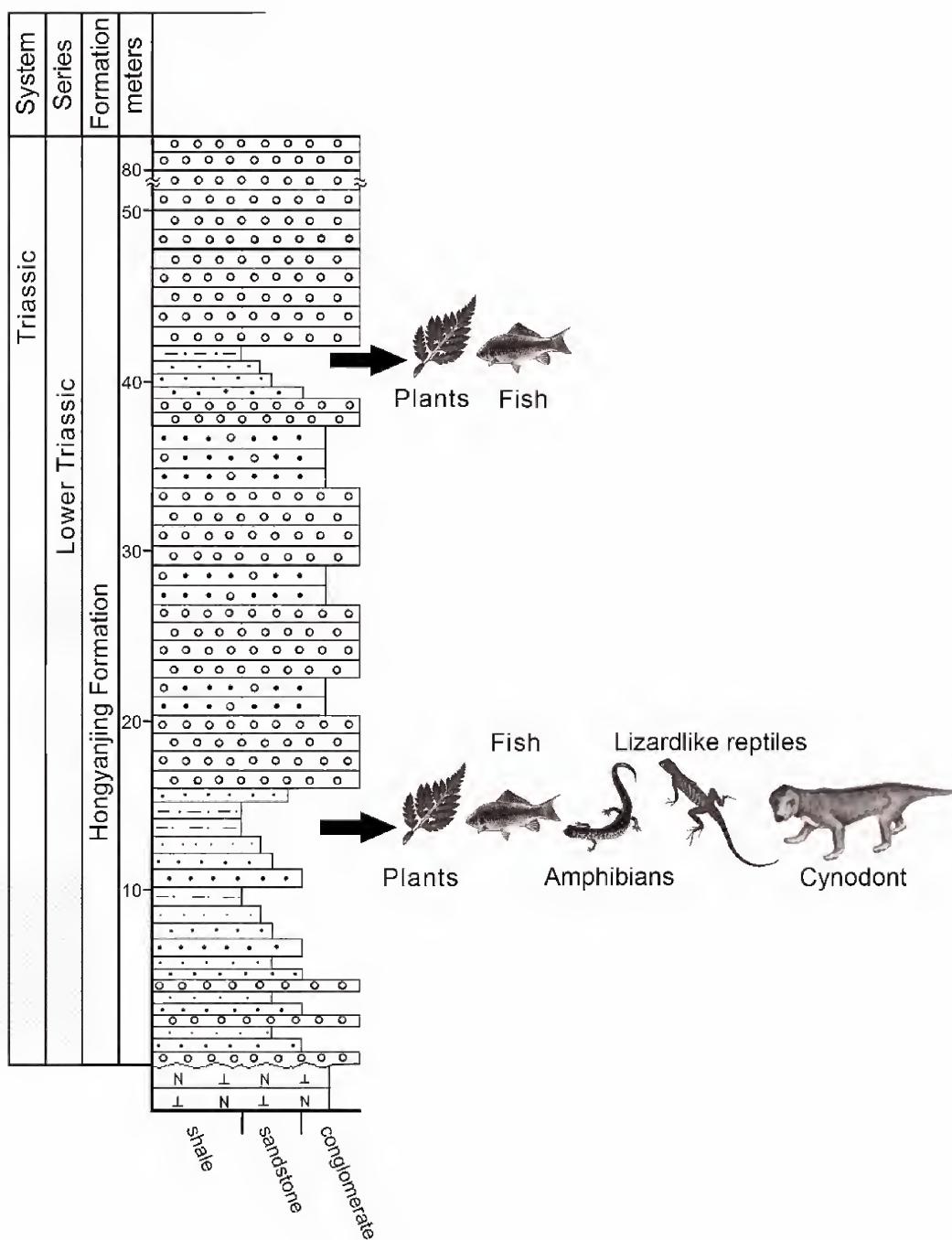


Fig. 2. Composite section of the Hongyanjing Formation exposed in the Beishan Hills. The new trirachodontid fossil was collected from the fossil-bearing dark shale exposed approximately 13.5 m above the basal contact of the formation with Hercynian plagioc-diorite rocks.

KNOWN DISTRIBUTION: Early to Middle Triassic, northern China.

SUBFAMILIAL DIAGNOSIS: Differing from other trirachodontid eucynodonts by possession of the following derived character states: snout shorter than temporal region; orbit subcircular, facing anteriorly; zygomatic arch strongly bowed laterally in keeping with greatly expanded temporal fenestra; zygomatic process of jugal absent; parietal foramen absent; temporal opening greatly expanded laterally; oblique inclination of last upper postcanine in relation to axis of skull (independent occurrences in some but not all traversodontids).

REMARKS: Because the two genera, *Sinognathus* and *Beishanodon*, share a set of derived character states that sharply set off the new clade from other trirachodontid eucynodonts, it is appropriate to name the new subfamily Sinognathinae. Within the infraorder Eucynodontia, the Sinognathinae form the sister group to the Trirachodontinae, which include the African genera *Trirachodon*, *Cricodon*, and *Langbergia* (Abdala et al., 2006; also see phylogenetic analysis and discussion below).

Beishanodon, new genus

TYPE SPECIES: *Beishanodon youngi*, new species.

ETYMOLOGY: After the Beishan Hills, in which the type locality occurs.

DIAGNOSIS: As for the type and only known species.

Beishanodon youngi, new species

HOLOTYPE: PKUP V3007, incomplete skull with well-preserved snout and left temporal region, but lacking the right zygomatic arch and much of the occiput; only known specimen.

ETYMOLOGY: The specific epithet is in honor of the late Chinese paleontologist C.C. Young, who named and described the first cynodont known from China.

TYPE LOCALITY AND HORIZON: Beishan locality, Quarry-3, in Beishan Hills ($41^{\circ}56'739''N$ / $96^{\circ}32'023''E$), northern Gansu Province, China; Lower Triassic dark shales of the Hongyanjing Formation (see above discussion).

DIAGNOSIS: An Early Triassic sinognathine trirachodontid differing from the closely related *Sinognathus gracilis* by the following derived characters: triangular lateral process of frontal closely approaching but not entering dorsal rim of orbit; jugal/postorbital suture located at midlength of postorbital bar; short intertemporal crest, about one-half length of enlarged temporal fenestra; posterior border of osseous secondary palate straight; incisor roots buccolingually expanded; upper canine obliquely positioned lateral to paracanine fossa; upper postcanine teeth eight in number, and less expanded laterally; transverse crest in upper postcanines located posteriorly; maxillary tooth row terminating at level close to anterior border of orbit; smooth curvature from snout to zygomatic arch; major palatine foramen penetrating palatine at midlength of the element.

DESCRIPTION

The holotype of *Beishanodon youngi* (PKUP V3007; figs. 3, 4) consists of an incomplete, somewhat dorsoventrally crushed skull lacking the mandibles. The well-preserved part of the skull includes a nearly complete snout and osseous secondary palate, most of the left temporal region, and a large part of the braincase floor. Several postcanine teeth are in place and show the characteristic transverse expansion of postcanines of gomphodonts. Most of the right side of the zygomatic arch and much of the occiput is missing. The skull is approximately 270 mm long from the tip of the snout to the posterior extremity of the temporal region. The completely preserved left zygomatic arch has a maximum width of 95 mm from the midline, and this measurement implies a maximum width of 190 mm across the greatly expanded zygomatic arches. The snout is extremely short (90 mm from its tip to the anterior border of the orbit), being one-third of the entire skull length as in *Sinognathus gracilis* (K.-Q. Gao, personal obs. of IVPP V2339: 42/122 mm). The orbit is small (with a diameter of roughly 25 mm) and faces mostly anteriorly. The temporal opening is greatly expanded laterally and posteriorly, in keeping with the strong lateral bulging of the zygomatic arch as a derived

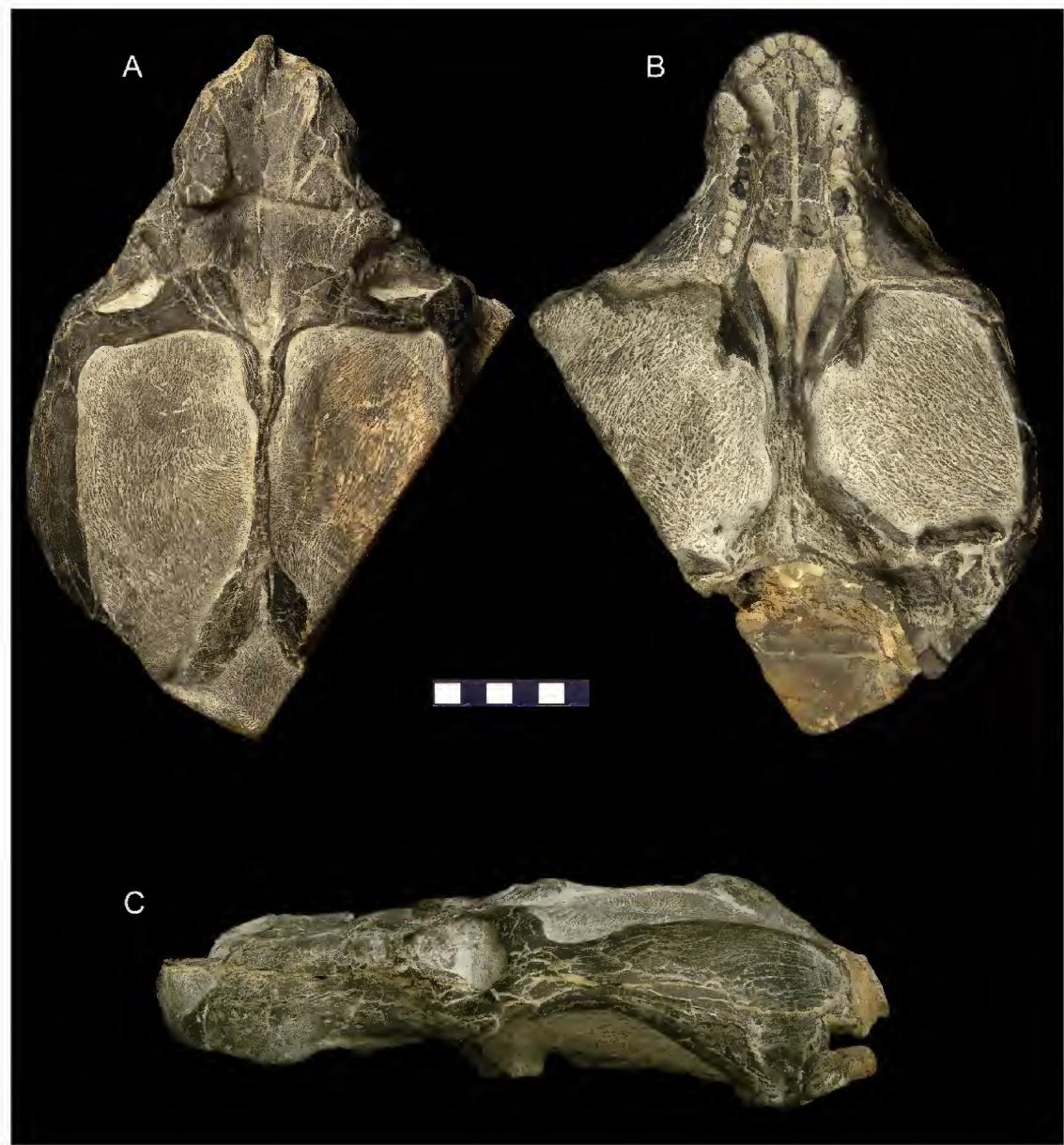


Fig. 3. *Beishanodon youngi*, gen. et sp. nov. (holotype PKUP V3007): skull in dorsal (A) ventral (B), and lateral (C) views.

feature shared with *Sinognathus gracilis*. The maximum width of the skull at the temporal region (~190 mm) is greater than twice the length from the tip of the snout to the posterior border of the secondary palate (80 mm).

SKULL ROOF: The premaxillae are paired, with a clearly evident sutural contact between

them along the midline. The premaxilla sends a slender internasal process first dorsally then turning posteriorly to separate the external nares; the tips of these processes continue posteriorly past the level of the nares to intervene for a short distance between the nasals. As shown on the right side of the specimen, the septomaxilla is exposed along the

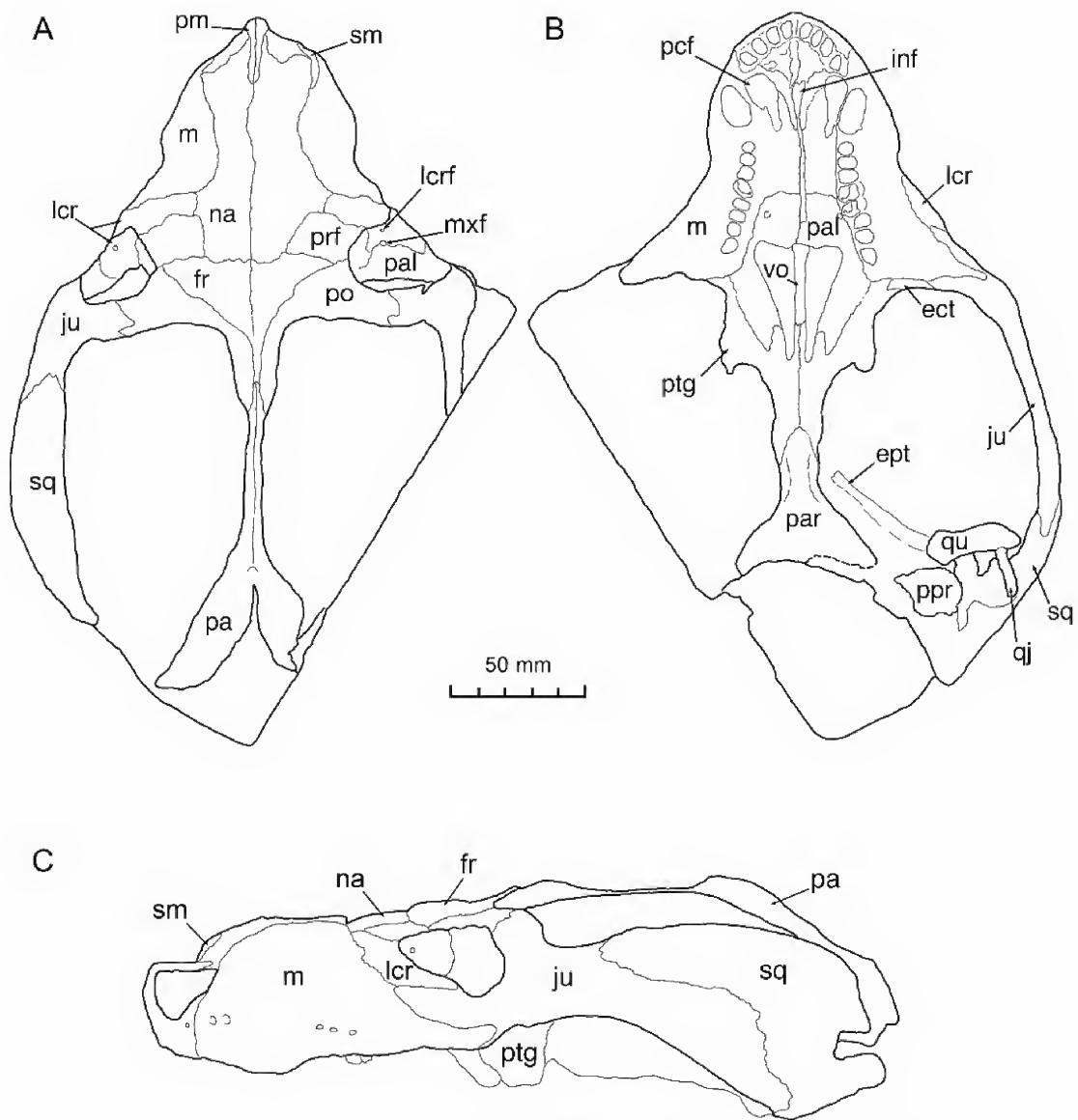


Fig. 4. *Beishanodon youngi*, gen. et sp. nov. (holotype PKUP V3007): line drawings of skull in dorsal (A), ventral (B), and lateral (C) views.

lateral border of the external narial opening and prevents the maxilla from contributing to the border of the opening. A splintlike dorsal process of the septomaxilla is wedged between the anterodorsal margin of the maxilla and the nasal (fig. 4A, C). A septomaxillary foramen normally developed at the suture between the septomaxilla and the maxilla in primitive synapsids (Kielan-Jaworowska et al., 2004) is not evident in this specimen.

The nasals are paired, wide, and posterolaterally contact both the lacrimal and the prefrontal as in other cynodonts (Kemp, 1982). The anterior border of the nasal appears to be slightly notched for the external naris although this edge is damaged bilaterally; the naris faces more anteriorly than laterally. The width of the nasals at the posterior borders of the narial openings is about 40 mm; more posteriorly, these bones

are slightly constricted with their concave lateral borders meeting the dorsal edges of the maxillae. Further posteriorly, the nasals widen again to a maximum total width of roughly 50 mm opposite the anterior border of the orbits. The nasal terminates posteriorly at a transverse suture with the frontal and posterolaterally along an oblique suture with the prefrontal; the nasofrontal suture is opposite the midlength of the orbits. A suturelike transverse line crosses the nasals and extends laterally into the posterodorsal border of the maxillae on both sides of the specimen; this feature, however, is a fracture and hence only an artifact of preservation.

Between the orbits, the paired frontals form a broad triangular plate with its apex pointing posteriorly. The dorsal surface of the plate is deeply depressed along the midline suture. The surface lining this depression is rugose and may reflect the attachment of some accessory structure, perhaps epidermal scutes or other ornamentation, or a soft-tissue crest. Lateral to the transverse suture with the nasal, the frontal is developed as a triangular process that closely approaches but does not enter the dorsal rim of the orbit, blocked by the contact between prefrontal and postorbital. Posteriorly, the frontal narrows to a slender process that, with its counterpart, is wedged between the posteromedial processes of the postorbitals and articulates with the parietals in the anterior extremity of the intertemporal crest.

As seen in other eucynodonts, the parietals in PKUP V3007 meet at the midline to form most of the intertemporal crest. The length of the crest, however, is only about one-half the length of the enlarged temporal fenestra. Such a proportionally short intertemporal crest is obviously different from that in *Sinognathus gracilis*, in which the crest extends to the level of the posterior border of the temporal opening (Young, 1959: fig. 1, pl. 1; Sun, 1988: fig. 1). A parietal foramen is absent in PKUP V3007, as in *Sinognathus gracilis*; other trirachodontids retain the foramen, although a single species, *Trirachodon berryi*, is known to be polymorphic in this character (Abdala et al., 2006). The parietal sends a well-developed flange ventrally to form a large part of the medial wall of the temporal fossa. Postero-laterally, a thickened posttemporal process of

the parietal diverges from the intertemporal crest and runs posteroventrally toward the posterior extremity of the temporal fenestra. Even on the better-preserved left side of this specimen, the posteriormost rim of the fenestra is damaged, and the sutural pattern of the parietal-squamosal contact cannot be determined.

In keeping with the proportions of the snout of PKUP V3007, the maxilla, which is well preserved on both sides of the skull, is short and deep. In lateral view, the anterior border of the maxilla meets the premaxilla along an anteriorly convex, nearly vertical suture (figs. 3C, 4C); above this contact, the dorsal process of the septomaxilla is exposed on the right side of the skull. The high dorsal margin of the maxilla is subarcuate from anterior to posterior, and although now somewhat fractured, it probably bent slightly medially to meet the concave lateral border of the nasal. The lateral surface of the maxilla is mostly smooth, and is swollen for reception of the large canine root (canine eminence; fig. 5). A horizontal row of small nutritive foramina opens externally above the ventral border of the maxilla. As seen on the right side of the skull, an infraorbital foramen is located at the level of the fourth postcanine tooth and oriented mostly anteriorly. On the right but not the left side of the snout, where the lateral surface is damaged by a horizontal crack, there is no evidence of this foramen. According to Abdala et al. (2006: character 22), a labial platform of the maxilla arises lateral to the postcanine series in the South African trirachodontids *Trirachodon* and *Cricodon*, but not in *Langbergia*. In PKUP V3007, such a platform is well developed, forming a distinctive triangular surface at the base of the snout and beneath the orbits (figs. 3, 5). The lateral extension of this platform ends just anterior to the anterolateral corner of the subtemporal fenestra as also seen in *Sinognathus gracilis* (Young, 1959: pl. 1).

The lacrimal is well developed, forming the anterior wall and the anterolateral border of the orbit (fig. 4A, C). As exposed on the right side, two foramina are associated with this bone: a small lacrimal foramen opens close to the anterodorsal border of the orbit, and a much larger and more ventrally located maxillary foramen is located at the suture



Fig. 5. *Beishanodon youngi*, gen. et sp. nov. (holotype PKUP V3007): CT-scan of the holotype skull showing tooth sockets and palatal structures (the scanning of the specimen was done by using a GE Light-Speed QX/I CT Scanner at the Peking University People's Hospital). Anterior arrows point to the canine eminence, and posterior arrows point to the oblique orientation of the last postcanine.

between the lacrimal and the orbital plate of the palatine (fig. 4A); the maxillary foramen represents the posterior entrance to the infraorbital canal. The lacrimal bone meets the prefrontal and the nasal dorsally, the maxilla anteriorly, the orbital plate of the palatine ventrally, and the anterior process of the jugal ventrolaterally, on the side of the face beneath the orbit (fig. 4A, C).

In dorsal view, the prefrontal is developed as a small rectangular bone that forms the anteromedial part of the orbital rim; anteriorly, it meets the lacrimal, and more medially, it has a sutural contact with the nasal. The size and location of the prefrontal

in PKUP V3007 concur with that in Young's (1959: fig. 1) illustration of the skull of *Sinognathus gracilis*, but not with Sun's (1988: fig. 1) figure of the same specimen; Young's figure is correct (K.-Q. Gao, personal obs. of IVPP V2339). Posterolaterally, the prefrontal has a short contact with the postorbital, and this contact prevents the lateral process of the frontal from entering the dorsal border of the orbit. The postfrontal is absent as in other cynodonts (Romer, 1956).

The lateral process of the postorbital meets the dorsal process of the jugal to form the robust postorbital bar separating the orbit from the temporal fenestra. The suture be-

tween the two bones is approximately at the midlength of the bar, differing from the more lateral position of this suture in *Sinognathus gracilis* (see Young, 1959: fig. 1). Medially, the postorbital has an extensive sutural contact with the frontal; a posteromedial process of the postorbital is developed as a vertical crest that extends to surpass the posterior process of the frontal and meet the parietal. Anteromedially, the postorbital articulates with the prefrontal to complete the dorsal rim of the orbit.

The jugal, as shown by the nearly completely preserved left element, is a stoutly built, quadripartite bone. The well-developed dorsal process joins with the postorbital to complete the postorbital bar as described above. In lateral view, the anteroventral process of the jugal is similar in length but slightly narrower than the dorsal process. It rests on the dorsal edge of the posterior process of the maxilla and anterodorsally meets the lacrimal to complete the ventral border of the orbit. A variable number of small foramina are developed along the maxillary/jugal suture in the South African *Trirachodon* and *Langbergia* (Abdala et al., 2006), but comparable openings are not seen in PKUP V3007. The suture between the jugal and squamosal within the zygomatic arch in lateral view begins anterodorsally close to the anterior border of the temporal fenestra, runs obliquely to the midlevel of the fenestra, and then turns posteroventrally toward the lateral side of the craniomandibular joint, where the posterior extremity of the jugal fits into a small ventral notch of the squamosal. The ventral border of the jugal is smoothly curved, concave dorsally, and lacks a suborbital process (figs. 3C, 4C). In ventral view, a slender anteromedial process of the jugal runs medially along the anterior border of the subtemporal fenestra; it meets the greatly reduced ectopterygoid, preventing the maxilla from entering the border of the fenestra (fig. 4B).

The squamosal is nearly completely preserved on the left side, with only its posterior tip missing. The zygomatic arch is deep and is composed of the jugal and squamosal (fig. 4C); within the arch, the squamosal is more heavily built than the jugal and has a

much more extensive lateral exposure. A robust anterior process of the squamosal extends dorsal to the posterior process of the jugal, reaching a point anteriorly that is close to the anterior corner of the temporal fenestra. Posteriorly, the squamosal extends ventrally to contact the quadrate condyle as in *Sinognathus gracilis* (Sun, 1988) and some other eucynodonts (Kemp, 1982: figs. 70, 83, 85).

CRANIOMANDIBULAR JOINT: Although the lower jaw is missing, the jaw suspensorium is well preserved on the left side of the skull (fig. 4B). The quadrate condyle, which is transversely elongated, is exposed. The condyle is laterally embraced by the squamosal and is posterolaterally reinforced by the quadratojugal, which is reduced to a small splint fitting into a notch of the squamosal. Such a quadrate-quadratojugal complex attached to the squamosal is a primitive pattern for cynodonts (Kemp, 1982; Kielan-Jawarowska et al., 2004).

OSSEOUS SECONDARY PALATE: The pattern of the palatal bones is well displayed in PKUP V3007 as revealed by computed tomography and subsequent manual preparation of the specimen. The osseous secondary palate is well developed, with contributions from the palatal process of the paired premaxillae and maxillae, and from the palatines (fig. 4B). The osseous secondary palate includes no fenestrae, but a small, fissurelike incisive foramen (of Abdala et al., 2006; “vomerine fossa” of Tatarinov, 1968) is developed anteriorly at the midline. This foramen opens anteriorly at the level of the posteriormost incisors and extends to the posterior level of the canines. The incisive foramen is mostly bordered by the premaxillae, but is closed posteriorly by the maxillae. Anteromedial to the enlarged canine, a deep depression, the paracanine fossa (e.g., Abdala et al., 2006), which received the lower canine when the mandible was adducted, is developed on either side of the osseous secondary palate.

The palatal process of the maxilla extends medially to form the major part of the osseous secondary palate, comprising nearly two-thirds of the palatal area anterior to the choanae. The palatines make up the posterior third of the osseous secondary palate

and form a straight posterior rim that delimits the choanae ventrally. Laterally, the palatine meets the maxilla along a straight oblique suture that runs medial to the posteriormost five postcanine teeth. The palatine then continues posteriorly and posterolaterally to a contact with the pterygoid posterior to the secondary palate on either side of the dorsal nasopharyngeal trough that extends posteriorly from the choanae (Barghusen, 1986). A major palatine foramen is present, but unlike that in other known cynodonts, it penetrates the palatine at the level of the fourth postcanine tooth from the rear and toward the lateral margin of the bone, rather than more anteriorly, at the transverse maxillary-palatine suture.

The straight posterior margin of the osseous secondary palate in PKUP V3007 differs from that in *Sinognathus gracilis* and many other eucynodonts, in which this margin is anteriorly concave (Sun, 1988; Kemp, 2005). A posteriorly extensive osseous secondary palate having a straight posterior border as in PKUP V3007 represents a more derived state than in many other eucynodonts (see Kemp, 2005, for figures of the osseous secondary palate in *Cynognathus*, *Thrinaxodon*, and *Massetognathus*), in which the posterior border is anteriorly concave and ends at a level anterior to the posteriormost maxillary tooth (see Kielan-Jaworska et al., 2004; Kemp, 2005).

The vomers are fused in PKUP V3007 to form a single median element in support of the osseous secondary palate, as in all other cynodonts with the possible exception of the Permian *Dvinia* from Russia (Tatarinov, 1968; Kemp, 1979, 1982; but see Battail, 1982; Hopson and Barghusen, 1986; Hopson, 1991). The anterior extremity of the median vomer is narrowly exposed within the incisive foramen; the vomer is more extensively exposed posterior to the choanae, where it forms a well-developed midline girder. This girder divides the nasopharyngeal trough and extends posteriorly to meet the pterygoids toward the posterior end of the trough (figs. 3B, 4B, 5).

The ectopterygoid is greatly reduced to a small bone occupying the more medial parts of

the anterior border of the subtemporal fenestra. It articulates with the posterior border of the maxilla between the pterygoid and the curved anteromedial process of the jugal, and thereby prevents the maxilla from entering into the anterior border of the subtemporal fenestra. There is no ectopterygoid foramen.

Posterolateral to the palatine, the pterygoid is developed into a strong descending flange that projects ventrally at the anteromedial border of the subtemporal fenestra. At the base of the flange, the pterygoid meets the palatine in an elongate suture within a trough lateral to the pterygopalatal ridge; this ridge forms the lateral border of the nasopharyngeal trough. The pterygoid continues further posteriorly, past the palatine to meet its counterpart in a median pterygoid ridge, which anteriorly contacts the fused vomer (figs. 3B, 4B). An anterolateral extension of the pterygoid at the base of the descending process meets the posterior border of the maxilla, then curves laterally to meet the greatly reduced ectopterygoid at the anteromedial corner of the subtemporal fenestra.

BRAINCASE: A large part of the braincase floor is exposed ventrally, with the posterior part missing owing to breakage (fig. 4B). The lateral wall of the braincase is not yet exposed. As in other cynodonts, the parasphenoid is elongate and is much wider than the parietal skull roof at the intertemporal crest. This indicates a narrowly triangular cross section for much of the endocranial cavity, although the lateral wall of the braincase is not exposed for observation. Compared to the holotype of *Sinognathus gracilis*, the parasphenoid of the new taxon has a much wider rostrum and much greater posterolateral expansion of the basal plate of the element, differing from the simple triangular configuration of the cranial base in *Sinognathus gracilis* (K.-Q. Gao, personal obs.; also see Young, 1959: pl. 1, contra Sun, 1988: fig. 1). The paroccipital process is partly exposed on the left side of the holotype; its lateral end contacts the squamosal and may also have a small contact with the medial side of the quadrate. The basioccipital and occipital condyles are not preserved.

The lateral wall of the braincase is not fully exposed for observation, but the epipterygoid is ventrally exposed as a well-developed crest

lateral to the parasphenoid. The posterior extension of the bone contacts the quadrate, a primitive condition among cynodonts as seen in *Procynosuchus* and *Dvinia* (Kemp, 2005), and the anterior extension probably contacts the pterygoid, although this part of the bone is broken on the left side of the specimen.

DENTITION: The upper dentition consists of four incisors, an enlarged canine, and eight postcanines in each jaw (figs. 3B, 4B, 5). Previous phylogenetic analysis (Abdala et al., 2006) has shown that four upper incisors is a plesiomorphic feature that is widely distributed among eucynodonts; the derived state of three upper incisors is confined to a few traversodontid genera (see Phylogenetic Discussion below). Although the upper incisors are not preserved in PKUP V3007, their alveoli are oval, suggesting that the roots and hence the crowns were buccolingually expanded. If so, they would have differed from the more nearly circular cross section of the roots and occlusal outline of the crowns displayed by the upper incisors of *Sinognathus gracilis* (see Young, 1959; Sun, 1988).

As in *Sinognathus* and numerous other cynodonts, a short diastema intervenes in PKUP V3007 between the posteriormost incisor and the canine (figs. 3B, 4B, 5). The alveolus of the canine is large and elliptical, and is oriented at an oblique angle, having its long axis extending from anterolateral to posteromedial. This obliquely oriented alveolus is positioned more laterally than posteriorly to the paracanine fossa, implying that the lower canine would have had a limited lateral exposure when the jaws are closed.

The postcanine teeth, as clearly shown on both sides of the skull, are arranged in a virtually straight line in each row, with the two rows slightly diverging posteriorly, but inset from the overhanging buccal maxillary shelf as in other gomphodonts and even in tritylodontids (Hopson, 1991). A short diastema, slightly longer on the right than on the left, separates the canine from the anteriormost postcanine tooth. The long axis of the postcanine tooth row is directed toward the center of the subtemporal fenestra (figs. 3B, 4B), a synapomorphy of trirachodontids (Abdala et al., 2006).

Like the incisors and canines, much of the postcanine upper dentition in PKUP V3007 is known only from alveoli, but the first four postcanines on the right are in place in the specimen and clearly demonstrate their coronal morphology (fig. 6A). In addition, the fourth and fifth postcanines on the left are preserved, but these are badly damaged, showing no details of the crown pattern (fig. 6B). In contrast to *Sinognathus gracilis*, the upper dentition of PKUP V3007 ends at a level beneath the anterior border of the orbit, although having a greater number of postcanine teeth (eight) than the former taxon, which had seven.

In PKUP V3007, the first postcanine tooth, which is preserved on the right side, has a columnar root and is substantially smaller than the more posterior postcanines. Its crown is subcircular in occlusal outline; a small cusp arises in the center of the crown, while a much larger cusp is developed labially. The crown displays weakly developed anterior and posterior crests or cingula, each bearing two to three small cuspules, but those on the posterior crest are clearly larger than the anterior ones. The second through the seventh teeth are increasingly expanded transversely, although substantially less so than are the comparable postcanines in *Sinognathus gracilis*. The crowns of the second through fourth teeth are elliptical in occlusal outline (fig. 6A). Their crown patterns differ slightly from that of the first postcanine in having a well-defined transverse crest located posteriorly on the crown. Three cusps are developed along the transverse crest, with the central cusp close to the middle (fig. 6A). The fourth right postcanine shows a well-defined posterior cingulum carrying up to 10 small cusps (fig. 6A). The last upper postcanine is not preserved on either side of PKUP V3007, but the alveolus at this tooth position is set at an oblique angle (roughly 45°) in relation to the axis of the tooth row (fig. 5).

PHYLOGENETIC ANALYSIS

Abdala et al. (2006) presented a phylogenetic analysis of trirachodontid eucynodonts, based on a data set of 43 characters coded across 18 taxa (Abdala et al., 2006: appendices 1–3). Their analysis using the computer



Fig. 6. Tooth morphology of *Beishanodon youngi*, gen. et sp. nov. (holotype PKUP V3007): A, occlusal view of first through fourth right postcanines; B, occlusal view of fourth and fifth left postcanines. Double arrows point to small cusps on posterior cingulum. Scale bar = 50 mm.

program TNT (Goloboff, 1999) generated 40 trees with an equal length of 103 steps, and the consensus of these trees shows unresolved relationships of several taxa as polytomies (Abdala et al., 2006: figs. 12, 13). Abdala et al.'s (2006) published data matrix contained incorrect alignment of character codings (Rubidge and Abdala, personal commun., 2008), and rerunning this published dataset does not produce the trees that Abdala et al. (2006) presented. Fortunately, a more recent publication by Kammerer et al. (2008) has made corrections of Abdala et al.'s data matrix, and we used the new dataset to build ours for this study (see appendices 1 and 2).

In this study, we have expanded the dataset of Kammerer et al. (2008) by incorporating the two taxa from China (*Sinognathus* and *Beishanodon*) and adding several characters from other sources (see appendix 1). Analysis of the revised dataset (appendix 2) was performed using branch-and-bound search option in PAUP* 4.0b for Mac (Swofford, 2002). Tracing of character evolution was enhanced using MacClade version 4.05 for OS X (Maddison and Maddison, 2002). All characters were equally weighted, and multi-state characters were ordered to avoid possible loss of phylogenetic information (Merck, 1997; Wiens and Etheridge, 2003). Character

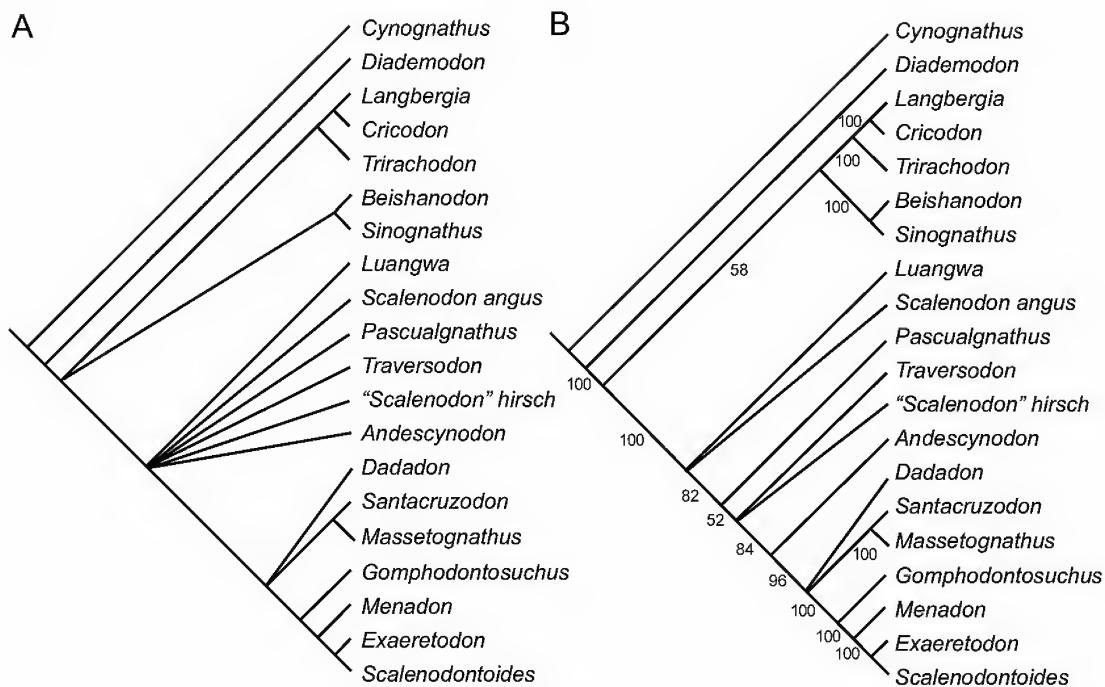


Fig. 7. Phylogenetic relationships of trirachodontid eucynodonts within Gomphodontia resulted from analysis of the revised dataset: A, Strict consensus of 67 MPTs (TL = 127 steps, CI = 0.520, RI = 0.712, RC = 0.37). B, 50% majority-rule consensus of the 67 MPTs; note the grouping of the Trirachodontinae with the Sinognathinae in the family Trirachodontidae gains a 58% support.

49 was uninformative, and thus was excluded from the analysis. The analysis resulted in 67 most parsimonious trees (MPTs), each having a length of 127 steps (CI = 0.520, RI = 0.712, RC = 0.370). The strict consensus of these MPTs shows that both Trirachodontinae and Sinognathinae are well supported as monophyletic clades, but the two clades ended with Traversodontidae (see Flynn et al., 1999, for a different definition of the family) as a trichotomy in the strict-consensus tree (fig. 7A). Several traversodontids are also involved in unresolved polytomies and show the same topology as in Kammerer et al. (2008: fig. 15A). Because of the poor resolution of the strict-consensus tree, 50% majority-rule consensus was performed to provide an alternative resolution of some unresolved clades (fig. 7B). The grouping of the Trirachodontinae and Sinognathinae gains 58% support, while grouping the selected 13 taxa in the Traversodontidae gains 100% support.

Within the phylogenetic framework, the grouping of the new taxon with *Sinognathus*

as sister taxa is unambiguously supported by the following characters:

- (24-1) Parietal foramen in adults absent (convergent in several traversodontids).
- (25-3) Zygomatic process of jugal absent (convergent in *Santacruzodon* and *Dadadon*).
- (29-2) Snout substantially shorter than temporal region (a uniquely shared derived character state within the phylogenetic framework).
- (46-1) Posterior end of the secondary palate roughly at the same level as the anterior border of the orbit (convergent in *Exaeretodon*).

The *Sinognathus-Beishanodon* clade (the new subfamily Sinognathinae as named in this paper) is further placed as the sister group of Trirachodontinae (= Trirachodontidae in Abdala et al., 2006). This phylogenetic placement is supported by four shared derived character states that are recognized herein as diagnostic of the family Trirachodontidae:

- (17-2) Overall morphology of lower postcanines in occlusal view ovoid-elliptical.
- (34-1) Temporal fenestra having same width throughout its length (independent occurrence in some traversodontids).
- (37-1) Axis of the posterior part of maxillary tooth row directed toward the center of the fenestra.
- (38-2) Postcanine tooth row in adults formed by gomphodont and sectorial teeth (equivocal, because posterior teeth are not preserved in PKUP V3007).

Abdala et al. (2006) recognized two characters as diagnostic of their Trirachodontidae (= Trirachontinae in this paper), and these as listed in this paper are:

- (19-1) Three cusps in the transverse crest of the lower postcanines.
- (43-1) Shearing planes between the outer surface of the main cusp of the lower and the inner surface of the main cusps of the upper postcanines absent.

Both characters cannot be confidently scored for *Sinognathus* and are unknown for *Beishanodon*. Lack of information on character 19, in congruence with several above-mentioned characters (24-1, 25-3, 29-2, 34-1), places the *Sinognathus*-*Beishanodon* clade outside the Trirachontinae, and thus, necessitates the naming of the new subfamily Sinognathinae.

The *Beishanodon*-*Sinognathus* clade shares with some but not all traversodontid eucynodonts several character states, as follows:

- (9-1) The last upper postcanine is oblique in relation to the axis of the skull (shared with all but four genera of traversodontids—*Luangwa*, *Scalenodon*, *Pascualgnathus*, and *Andescynodon*).
- (24-1) Parietal foramen in adults absent (independent occurrences in several traversodontids).
- (25-1) Zygomatic process of jugal absent (independent occurrences in several traversodontids).

Parsimony analysis of the entire dataset, however, implies that the derived states of these three characters are independently evolved within the Trirachodontidae and Traversodontidae. Recognition of the Sinognathinae and Trirachontinae as sister subclades within the

Trirachodontidae is corroborated by the biogeographic distribution of the members of these two subfamily groups: members of the Sinognathinae are entirely Asian and those of the Trirachontinae are African in distribution (see discussion below).

Within the Traversodontidae, *Scalenodon angustifrons* and “*Scalenodon*” *hirschsoni* are consistently placed as non-sister groups as in previous analyses (Abdala et al., 2006; Kammerer et al., 2008). Manually forcing the sister-taxon grouping of these two forms would increase tree length by six steps (127 steps vs. 133). This result gives a strong indication that the latter taxon needs to be revised, but such a study is beyond the scope of this paper.

STRATIGRAPHIC AND BIOGEOGRAPHIC DISCUSSION

The discovery of the new eucynodont from northern Gansu Province of China has significant biostratigraphic implications. Because trirachodontids have a limited temporal range of Olenekian-Anisian (Abdala et al., 2005, 2006), the new fossil trirachodontid from Gansu provides definitive evidence for biostratigraphic correlation of the Beishan beds with the South African *Cynognathus* Assemblage Zone (AZ); the *Cynognathus* AZ is the standard biozone for comparison of the continental Triassic worldwide. Within the *Cynognathus* AZ, three informal subzones A-C have been proposed primarily based on temnospondyl amphibians as key fossils (Abdala et al., 2005). The Beishan beds have yielded no temnospondyls comparable to those from South Africa, but all other biostratigraphically informative groups—hybodont sharks, actinopterygians, and plants—are consistent with an Early Triassic age (see Introduction above). Based on the information furnished by the vertebrate fauna, we interpret the age of the Beishan beds to be late Early Triassic (Olenekian).

Determination of the age of the Beishan beds leads to consideration of the age of the Ermaying Formation in Shanxi Province, owing to the occurrence of *Sinognathus gracilis* there (fig. 1). Young (1959) correlated the *Sinognathus* fossil-bearing horizon of the Ermaying Formation with the *Cynognathus* Assemblage Zone (AZ) of South Africa, and



Fig. 8. Biogeographic distribution of Trirachodontidae (data on African taxa from Abdala et al., 2006; base map from <http://www.theodora.com/maps>): South Africa—*Trirachodon*, *Langbergia*, *Cricodon* (Olenekian and Anisian); Namibia—*Trirachodon* sp. (Anisian); Tanzania—*Cricodon* (Anisian); Gansu—*Beishanodon* (Olenekian); Shanxi—*Sinognathus* (Anisian); Donguz—questionable record of trirachodontid.

regarded the fossil horizon as “the upper most lower Triassic or the lower part of the Middle Triassic” (Young, 1959). Later recognition that *Sinognathus* is a member of the Trirachodontidae (Sun, 1988) does not change Young’s argument for the Triassic age of the Shanxi beds. At present, the age of the Ermaying Formation is considered Middle Triassic (Yang et al., 2000; Yin, 2003). The formation has yielded the dicynodonts *Sinokannemeyeria* and *Shansioidon* (Young, 1937; Yeh, 1959). Both are regarded as index fossils of the Perovkan Land Vertebrate Fauna (Gradstein et al., 2004; Rayfield et al., 2005); therefore, the Ermaying Formation is stratigraphically correlated with the subzone B and C of the *Cynognathus* AZ (Abdala et al., 2005), and is Anisian in age.

Trirachodontid eucynodonts have been discovered only in Africa and Asia (fig. 8). In Africa, *Cricodon*, *Trirachodon*, and *Langbergia* are known from South Africa, Namibia, and

Tanzania (Abdala et al., 2006). In Asia, until now the only known genera have been *Sinognathus* and the problematic form, *Neotrirachodon*, from Russia (see Introduction). Abdala et al.’s (2006) recent review confirmed the relationship of *Sinognathus* with the Trirachodontidae, but recognized the latter as only “Gomphodontia incertae sedis” (but see Battail and Surkov, 2000, as a bauriid; James Hopson and Bruce Rubidge, personal commun., 2008). The discovery of *Beishanodon* from northern Gansu Province, China, adds greatly to both the stratigraphic range and the biogeographic distribution of trirachodontids in Asia, extending the occurrence of the family to the Early Triassic, far to the northwest of *Sinognathus* in the Wuxiang area of Shanxi Province.

CONCLUSIONS

Recent fossil discoveries from the Early Triassic deposits exposed in the Beishan Hills,

Gansu Province, China, provide the material for recognition of a new genus and species of a trirachodontid eucynodont. The study of the new fossil from the Beishan Hills comes to the following conclusions:

- (1) The dark shale deposits exposed in the Beishan area represent a previously unrecognized depositional facies in the terrestrial Triassic System in China. The beds yielded a rich vertebrate fauna together with a fairly diverse flora. A large number of undisturbed fish and amphibian fossils indicate a permanent freshwater environment at the fossil locality.
- (2) The new discovery provides the fossil material for recognition of a new genus and species of eucynodont that can be classified in the family Trirachodontidae.
- (3) Within the family Trirachodontidae, the new taxon is grouped with the previously known Chinese taxon *Sinognathus gracilis* as sister groups in a new subfamily Sinognathinae.
- (4) The discovery of the new trirachodontid fossil provides the most reliable evidence for intercontinental comparison of the Beishan beds with the Early–Middle Triassic *Cynognathus* Assemblage Zone in South Africa. Based on the new trirachodontid and other stratigraphically informative vertebrate fossils, the Beishan beds are correlated with the subzone A of the *Cynognathus* AZ, and thus, are Olenekian in age.
- (5) The discovery of new fossil trirachodontid from Gansu extends the known distribution of the group from Shanxi Province to far western China.

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APPENDIX 1

Characters used in the phylogenetic analysis

The first 43 characters were the original data of Abdala et al., 2006 (modifications explained following the description of the relevant character); character 44 was added by Kammerer et al., 2008; and characters 45–50 were of our own research. Note the characters in this list are enumerated beginning with “1,” not “0” as in Abdala et al., 2006, and Kammerer et al., 2008.

1. Number of upper incisors: (0) four; (1) three.
2. Incisor size: (0) small; (1) large. *Sinognathus* has small incisors, while the condition in the new taxon is unknown.
3. Diastema between upper incisors and canine: (0) present; (1) absent. Both *Sinognathus* and *Beishanodon* show the plesiomorphic state (0) of this character.
4. Upper canine size: (0) large; (1) reduced. The new taxon *Beishanodon* is coded with the plesiomorphic state based on large alveoli of the canines in the holotype.
5. Lower canine size: (0) large; (1) reduced. The large paracanine fossae in the palate of the holotype clearly indicate a pair of large lower canines in the new taxon.
6. Position of paracanine fossae in relation to the upper canine: (0) anteromedial; (1) medial; (2) posteromedial. The osseous secondary palate in *Beishanodon* shows the anteromedial position of the paracanine fossa. The osseous secondary palate in *Sinognathus* is unknown, but the occlusion pattern of the upper and lower canines clearly indicates the anteromedial position of the paracanine fossa (Sun, 1988).
7. Overall morphology of the upper postcanines in occlusal view: (0) sectorial; (1) ovoid-elliptical; (2) rectangular-trapezoidal. *Sinognathus gracilis* shows an elliptical morphology of the upper postcanines (see Sun, 1988).
8. Shouldering in upper postcanines: (0) absent; (1) present. Both *Sinognathus* and the new taxon *Beishanodon* show that no shoulder is developed in the upper postcanines.
9. Inclination of the last upper postcanines in relation to the axis of the skull: (0) absent or small; (1) oblique. The alveolus of the last postcanine in PKUP V3007 shows an oblique position of the tooth in relation to the axis of the skull; thus, we coded the derived condition for *Beishanodon*.
10. Location of the transverse crest of upper postcanines: (0) central; (1) anterior; (2) posterior. Several upper teeth preserved in PKUP V3007 show a posterior location of the transverse crest.
11. Number of cusps in the transverse crest of the upper postcanines: (0) two; (1) three or more. *Sinognathus gracilis* shows the derived state as described and figured in Sun (1988: fig. 4). Because *Beishanodon* has up to three cusps on the transverse crest, we coded the derived state for the new taxon.
12. Central cusp of upper transverse crest: (0) midway between buccal and lingual cusps; (1) closer to lingual cusp; (2) close to labial cusp. The new taxon shows a more labial position of the central cusp; thus, we have added the state (2) to this character.
13. Posterior cingulum on upper postcanines: (0) present; (1) absent. The new taxon *Beishanodon* displays the plesiomorphic state of this character, while *Sinognathus* was described as having “a faint ridge lying parallel to the middle one, but without any cuspule” (Sun, 1988: 180).
14. External cingulum on the anterior portion of the upper postcanines: (0) absent; (1) present.
15. Anterolingual cusp in upper postcanines: (0) absent; (1) present.
16. Number of cusps in the sectorial border (i.e., labial margin) of the upper postcanines: (0) more than two; (1) two; (2) one. The new taxon has up to three cusps in the labial margin of the tooth crown, while the actual condition in *Sinognathus* cannot be ascertained.
17. Overall morphology of lower postcanines in occlusal view: (0) sectorial; (1) circular; (2) ovoid-elliptical; (3) quadrangular.
18. Position of the transverse crest in lower postcanines: (0) central; (1) anterior. The crown pattern of the lower postcanines in *Sinognathus* cannot be ascertained because the jaws are in occlusion (see Young, 1959; Sun, 1988).
19. Number of cusps in the transverse crest of the lower postcanines: (0) two; (1) three. The derived state diagnoses the Trirachodontinae. The lower postcanine teeth in *Sinognathus gracilis* have two cusps (Sun, 1988).
20. Size of the anterior cusps in the lower postcanines: (0) labial lower than lingual; (1) labial higher than lingual.
21. Anterior cingulum in the lower postcanines: (0) cuspules disposed on the entire margin; (1) one or more cuspules located anterolabially; (2) absent.
22. Internarial bar: (0) present; (1) absent. The condition of the internarial bar is unknown for *Sinognathus gracilis* (Young, 1959), but the bar is clearly present in the new taxon. As shown in Kammerer et al. (2008), the absence of the internarial bar is the derived state that

diagnoses the clade of *Scalenodontoides*–*Exaeretodon* within the Traversodontidae.

23. Maxillary labial platform lateral to the postcanine series: (0) absent; (1) present. Following Kammerer et al. (2008: character 22), three taxa (*Cynognathus*, *Diademodon*, and *Langbergia*) in the matrix were coded with the plesiomorphic state. Tracing of character evolution implies that the absence of the maxillary labial platform in *Langbergia* may represent a secondary loss.

24. Parietal foramen in adults: (0) present; (1) absent. Both *Sinognathus* and *Beishanodon* show the derived state of this character. This is one of the diagnostic features of the new subfamily Sinognathidae.

25. Zygomatic process of the jugal: (0) slightly projected; (1) conspicuously projected; (2) absent. Since Abdala et al. (2006: char. 24) concerns both presence/absence and the shape of the zygomatic process, we have chosen to break it down into two separate characters (chars. 25 and 26 in this paper). The presence of a zygomatic process of the jugal has been recognized as a cynognathian apomorphy (Rubidge and Sidor, 2001). Both *Sinognathus* (Young, 1959; Sun, 1988) and *Beishanodon* have lost the zygomatic process as a derived character state.

26. Posterior extension of the jugal above the squamosal in the zygoma: (0) absent or with a small extension; (1) well developed. Young (1959: fig. 3) figured the holotype of *Sinognathus gracilis* as having a long posterior extension of jugal below the squamosal, whereas Sun (1988: fig. 2) illustrated the same specimen as having a bifurcated posterior extension of the jugal that reached the posterior border of the temporal opening. Our personal observation of the holotype concurs with Young's original figure.

27. Coronoid process of the mandible: (0) covers the last postcanine in lateral view; (1) does not cover last postcanine. *Sinognathus gracilis* shows the plesiomorphic state of the character as Young (1959: fig. 3) figured. The condition is unknown for the new taxon.

28. Dentary angle: (0) not projecting posteriorly; (1) weakly projecting; (2) well projecting posteriorly. *Sinognathus gracilis* has a well-defined but weakly projecting dentary angle (angular process of the dentary in Sun, 1988: fig. 2; contra Young, 1959: fig. 3; K.-Q. Gao, personal obs. of IVPP V2339). This character is unknown for the new taxon.

29. Snout: (0) longer than temporal region; (1) subequal; (2) substantially shorter than temporal region. Modification of the original character description is made with adding of state (2) to reflect the derived condition in *Sinognathus* and *Beishanodon*.

30. Incisive foramen: (0) posteriorly closed by maxilla; (1) completely enclosed by premaxilla. The new taxon shows the plesiomorphic state of this character, while the actual condition is unknown in *Sinognathus gracilis* (Young, 1959; Sun, 1988).

31. Ectopterygoid: (0) present; (1) absent. Abdala et al. (2006: character 30) coded the absent condition for *Massetognathus*, contra Romer's (1967) illustration (see Abdala et al., 2006 for explanation).

32. Maxilla in margin of the subtemporal fenestra: (0) excluded; (1) included. The new taxon shows the primitive state of this character, whereas the condition is unknown for *Sinognathus*.

33. Epipterygoid-quadrate contact: (0) present; (1) squamosal interposed. The new taxon shows the primitive state of this character, while the condition is uncertain for *Sinognathus*. The derived condition is seen in *Exaeretodon* and *Massetognathus*, but is unknown for other traversodontids (Abdala et al., 2006: char. 32).

34. Temporal fenestra: (0) widest posteriorly; (1) same width throughout; (2) widest in the middle. Although having the temporal fenestra strongly expanded, both *Sinognathus* and the new taxon *Beishanodon* show a relatively straight lateral border of the fenestra; thus, we coded the derived state (1) of this character for the two Chinese taxa.

35. Incisor cutting margins: (0) serrated; (1) smoothly ridged; (2) denticulated. This character cannot be scored for *Sinognathus* or *Beishanodon* as a matter of specimen preservation.

36. Canine serrations: (0) present; (1) absent. This character cannot be scored for *Sinognathus* or *Beishanodon* because the canines are poorly preserved in the specimen of the former and not preserved in the latter.

37. Axis of the posterior part of maxillary tooth row: (0) directed toward the lateral rim of the subtemporal fenestra; (1) directed toward the center of the fenestra; (2) directed toward the medial rim of the fenestra. State (1) diagnoses the clade Trirachodontidae with inclusion of *Sinognathus* and *Beishanodon*. State (2) is diagnostic of the Traversodontidae.

38. Postcanine tooth row in adults: (0) formed by sectorial; (1) conical, gomphodont, and sectorial; (2) gomphodont and sectorial; (3) gomphodont only. Both *Sinognathus* and *Beishanodon* have gomphodont postcanines, but sectorial teeth are known for the former

(Sun, 1988: the sixth postcanine shows definitely sectorial feature) and unknown for the latter taxon.

39. Posterior cingulum in the lower postcanines: (0) present; (1) absent. This character is unknown for the new taxon, while the condition in *Sinognathus* is uncertain because the tooth rows are in occlusion.

40. Anterior cingulum in the upper postcanines: (0) present; (1) absent. The new taxon shows the plesiomorphic state, while the situation in *Sinognathus* is uncertain.

41. Deep occlusal basins in the postcanines: (0) absent; (1) present. The shallow basins as shown on the second through the fifth upper postcanines in PKUP V3007 are significantly different from what is seen in traversodontids; thus, we code the plesiomorphic state for the new taxon.

42. Postcanine occlusion: (0) absent; (1) present. All ingroup taxa with the upper and lower dentitions known are invariably coded with the derived state (1); thus, this uninformative character is excluded from the analysis.

43. Shearing planes between the outer surface of the main cusp of the lower and the inner surface of the main cusps of the upper postcanines: (0) present; (1) absent. The derived character state is known for the Trirachodontinae, and pending the condition in the two Chinese taxa it may be diagnostic for the clade Trirachodontidae.

44. Incisor procumbency: (0) absent; (1) present. This character was added by Kammerer et al. (2008) to Abdala et al.'s (2006) dataset. According to Kammerer et al. (2008), the derived state supports the grouping of [*Menadon* (*Exaeretodon* + *Scalenodontoides*)]. *Sinognathus* shows no procumbency of the incisors, but the actual condition is unknown for the new taxon.

45. Extent of maxillary tooth row: (0) essentially antorbital; (1) extending substantially suborbitally. Both *Sinognathus* and the new taxon *Beishanodon* show essentially the antorbital position of the maxillary tooth row, similar to *Trirachodon* and *Cricodon* but different from *Langbergia*, which has the tooth row extended almost halfway below the orbit.

46. Posterior extent of secondary palate in relation to the anterior border of orbit (Hopson and Kitching, 2001): (0) significantly anterior to the anterior border; (1) roughly at the same level as the anterior border.

47. Intertemporal crest in dorsal view: (0) extending to or close to posterior border of temporal fenestra; (1) shortening anteriorly with obvious posterior bifurcation. *Cynognathus* shows the primitive state of this character, while the similar conditions in *Langbergia* and *Sinognathus* apparently represent independent character reversals.

48. Major palatine foramen (from Kielan-Jaworowska et al., 2004): (0) at maxillary/palatine suture; (1) penetrating palatine.

49. Extent contribution of palatine to secondary bony osseous palate (from Kielan-Jaworowska et al., 2004): (0) far less than one-third of the palate; (1) more than one-third of the palate.

50. Posterior border of secondary palate in relation to maxillary tooth row (modified from Hopson and Kitching, 2001): (0) close to midlevel of postcanine tooth row; (1) close to posterior end of tooth row. According to Sun (1988), the posterior extension of the secondary osseous secondary palate is terminated at the level at the fourth and the fifth postcanines in *Sinognathus gracilis*. This concurs with Young (1959: fig. 2, pl. 1), who illustrated an arched posterior border of the secondary osseous secondary palate for *Sinognathus gracilis*.

APPENDIX 2
Taxon-character data matrix used in the phylogenetic analysis
(see appendix 1 for description of characters; A = 0/1, B = 0/2)

	5	10	15	20	25	30	35	40	45	50
<i>Cynognathus</i>	00000	00?0?	???0?	00???	?0000	00000	00000	0000?	00?00	00000
<i>Diademodon</i>	00000	01000	0?00?	0100?	00001	0A000	00000	00100	01000	01001
<i>Trirachodon</i>	00000	0100B	1A00?	2201?	001A1	00010	00010	01200	01100	01000
<i>Langbergia</i>	00000	01000	1000?	0201?	00001	01010	00011	01200	01101	00000
<i>Cricodon</i>	01000	01000	1100?	0201?	001??	010?0	20?0?	01200	01100	0??20
<i>Andesognathus</i>	00000	02001	0?10?	13101	10112	0?010	?001	12311	1100?	?????
<i>Massetognathus</i>	00111	121A2	11100	03100	20112	00011	10112	12300	11001	01100
<i>Exaeretodon</i>	11101	22112	0?101	03101	21111	10201	11111	12311	11011	11000
<i>Luangwa</i>	00000	01002	11010	A3100	10101	0010?	0?010	02300	11000	?????
<i>Scalenodon angus</i>	00000	0100B	11110	23100	10102	10?10	0?000	02301	1100?	?????
<i>Scalenodon hirsch</i>	1111?	020?	11001	13100	101???	?0000	1???	12300	1100?	?????
<i>Traversodon</i>	00000	02012	11011	13100	20101	00???	00???	123?	1100?	?????
<i>Gomphodondosichus</i>	00111	12112	0?10?	23101	201???	?0???	20?1?	12311	1100?	?????
<i>Pascualognathus</i>	10000	01000	0?0?0	231???	?110	0001?	0?01	123?0	11001	?????
<i>Scalenodontoides</i>	111???	221?	0?10?	03101	2111?	1021?	?1?21	?2311	1100?	?????
<i>Menadon</i>	01111	12112	0?101	2310?	201??	1020?	20?1?	02311	11011	?????
<i>Dadadon</i>	000??	02112	11111	2???	?01?3	?0???	?0???	123?1	11001	?????
<i>Santacruzadon</i>	000??	02112	11100	03101	201?3	?00??	?0???	12300	11001	?????
<i>Sinognathus</i>	00000	01010	10000	22?0?	?1111	20002	?0???	?12?	?01?0	10??1
<i>Beishanodon</i>	0?000	01012	12000	0???	?0111	20??2	00001	?1???	00??0	11111

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